Larval-damaged plants: source of volatile synomones that guide the parasitoid *Cotesia marginiventris* to the micro-habitat of its hosts

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Abstract

Single and dual choice tests in a flight tunnel revealed that plants damaged by host larvae are the main source of the volatiles that attract females of the parasitoid *Cotesia marginiventris* (Cresson) to the microhabitat of its hosts. Frass and host larvae, the other two major components of a complete plant-host complex, were significantly less attractive than the damaged seedlings; frass alone was more attractive than larvae alone. However, a recombination of larvae with the damaged seedlings was significantly more attractive than the damaged leaves alone, or damaged leaves with frass. This was due to the additional feeding damage done by the larvae. The role of plants in the host-finding behaviour of parasitoids is discussed.

Introduction

Numerous studies show that insect parasitoids are attracted to stimuli associated with their hosts (Vinson, 1976, 1981; Weseloh, 1981; van Alphen & Vet, 1986), and the majority of these stimuli appear to be of chemical origin. Volatile chemicals that attract parasitoids over long distances can be emitted by the hosts themselves (e.g., sex and aggregation pheromones) or by host by-products such as feces, silk, and honeydew. These host-derived allelochemicals that serve as cues for parasitoids are termed kairomones (for terminology see Nordlund & Lewis, 1976; Dicke & Sabelis, 1988a). Long-range chemical cues also can be released by plants upon which the host feeds (i.e., synomones), or by other organisms that are associated with the host or its habitat (Vinson, 1981; Weseloh, 1981; van Alphen & Vet 1986; Kainoh, 1987).

Cotesia marginiventris (Cresson) (Hymenoptera : Braconidae) is a generalist larval parasitoid that attacks many different lepidopterous species. This parasitoid responds vigorously (i.e., increase in klinokinesis) to contact kairomones present in the by-products of the host such as silk, saliva, and exuviae, but response is strongest to host feces and to the feeding damage caused by the host larvae (Loke & Ashley, 1984; Dmoch *et al.*, 1985). The females are attracted to the odours emanating from a complex of host larvae feeding on plants (Turlings *et al.*, 1989). However, the exact origin of the attractive volatiles was heretofore unknown. Indirect evidence obtained from

experiments on learning suggests that both the plant and the host are involved in the production of the active semiochemicals (Turlings *et al.*, 1990). In olfactometer tests, females prefer odours previously encountered during a contact experience. This preference is observed when females are given the choice between two odour sources each containing a different host species feeding on the same plant species, but also when the odour source contains two different plant species fed upon by the same host species. Apparently, both the host as well as the plant are involved in the production and/or release of the active volatiles. Here we present the results of a flight tunnel study in which the main source of the active allelochemicals was determined by testing different components of a complex of beet armyworm (BAW), *Spodoptera exigua* (Hübner), larvae feeding on corn seedlings for their attractiveness to females of *C. marginiventris*.

Methods and materials

The insects. Cotesia marginiventris were reared on fall armyworm larvae at the USDA/ARS, Insect Biology and Population Management Research Laboratory, Tifton, Georgia, as described by Lewis & Burton (1970) for *Microplitis croceipes* (Cresson). Cocoons were collected 2–3 days prior to emergence and mailed to Gainesville where they were kept in $25 \times 25 \times 25$ cm plexiglass cages, each with three sides of fine mesh nylon screen. The cocoons were transferred to a new cage each day thereby separating the wasps by age. Males were removed after two days. The cages were stored at 26 °C, 50–60% RH, and a 15 h photophase. All experiments were conducted with 3- to 5-day-old mated females, 6–10 h into the photophase. The hosts used in the experiments were late second or early third instar BAW larvae, reared as previously described by King & Leppla (1981).

Flight tunnel. Responses of *C. marginiventris* females to volatile chemicals emitted by different odour sources were observed in a plexiglass flight tunnel 60 cm × 60 cm in cross-section and 2.4 m long. Two sheets of nylon mosquito netting (10 cm apart) at the open upwind end and one sheet of nylon screen (7×7 mesh/cm^2) at the downwind end provided near laminar flow. Air was pulled through the tunnel at 0.2 m/sec and was exhausted via a 30 cm diam. flexible pipe with a fan. Four overhead incandescent lights (90 W) were dimmed so that they provided approximately 500 lux inside the tunnel. The room housing the tunnel was maintained at 27.5–29 °C and 55–80% RH. A more detailed description of the tunnel is given by Eller *et al.* (1988).

Odour sources. Corn seedlings (Ioana sweet corn) were grown in a greenhouse and cut for immediate use when 10–15 days old. Stems were wrapped in wet cotton wool and 12 seedlings were then placed in glass containers (26 cm in diam., 10 cm high) with 50 second instar BAW larvae. The following day (18–20 h later) various components of the plant-host complex were used as odour sources in the flight tunnel bioassays. To determine the actual source of attractive volatiles the complex was divided into three major components: 1) the host-damaged leaves; 2) frass; and 3) the host larvae. The frass was obtained by wiping it from three host-damaged seedlings using one wet and one dry piece of cotton wool. The seedlings were then water-washed to remove any remaining larval by-products. Fifteen host larvae that had been feeding on these leaves overnight were starved for 2 h to prevent them from defecating during the bioassays, and subsequently water-washed. These three major components of a complete plant-host complex were then used as odour sources in the flight tunnel tests, both in single choice and in dual choice situations. Several recombinations (described in the next section) of the three components were tested in additional dual choice tests to determine what combination of the three components is required for maximum attractiveness.

Odour release system. An odour source was placed in a glass cylinder dispenser (Fig. 1a) attached to a 0.5 cm-diam. stainless steel tube which entered
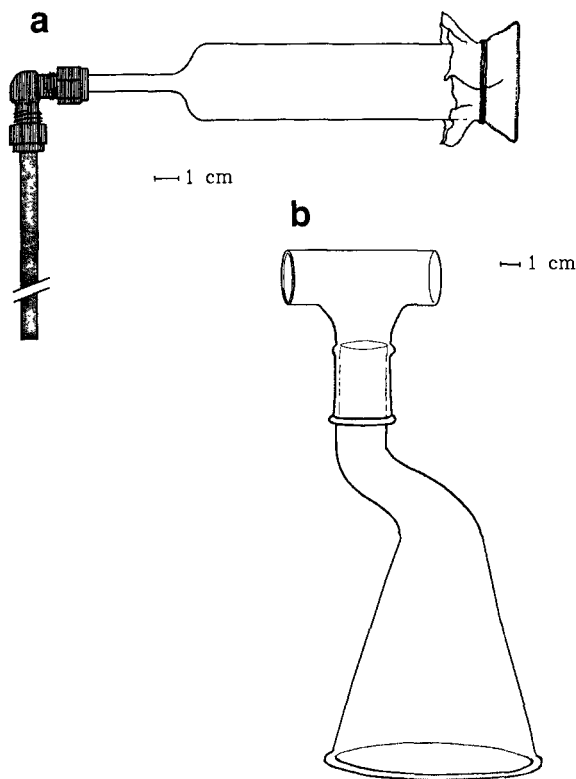
Fig. 1. (A) Odour inlet system. An odour source is placed in a glass chamber attached to a stainless steel 1/4″ tube 25 cm above the flight tunnel floor. The wide open end of the glass chamber is covered with fine mesh nylon screen, kept in place with a rubber band. Clean, humidified air is pushed through the stainless steel tube and the glass chamber at a rate of 0.5 l/min; - (B) Insect release funnel. Female wasps are placed under the glass funnel 80 cm downwind from the odour inlet system. Attraction to light will guide them to the open tube on top of the funnel 22 cm above the flight tunnel floor and in the trajectory of an odour plume. When attracted to the odour the wasps will take off from the funnel and fly upwind toward the odour source.

through the floor at the upwind end of the flight tunnel. The open downwind end of a cylinder was covered with a piece of nylon mosquito netting, held in place with a rubber band (see Fig. 1a). Humidified air was blown via the stainless steel tube through the cylinder at a rate of 500 ml/min to provide a continuous odour plume in the tunnel. For dual choice tests the stainless steel tube was split into a 'T' and a glass cylinder was attached to each end, 6 cm apart. With smoke sources it was determined that this system resulted in two distinct spiralling plumes that met 25 cm

downwind from the cylinders and overlapped approximately 80% at the wasp release point (80 cm downwind from the cylinder).

Bioassays. A 3- to 5-day-old *C. marginiventris* female was given a 20–40 sec contact experience with a complete plant-host complex (BAW larvae on corn seedlings on which they had fed overnight) during which she oviposited once or twice. This type of experience is known to increase responses to odours emitted by a plant-host complex significantly (Turlings *et al.*, 1989). The female wasp was then transferred into a 20 ml vial which was placed under a release funnel (Fig. 1b) inside the wind tunnel 80 cm downwind from the odour source. The female soon walked up the funnel toward the light and eventually reached the open tube on top of the funnel where she made initial contact with the odour plume. When attracted, the female would walk toward the upwind end of the tube, take off, and fly toward the odour source. Here, we only report on whether or not a female flew all the way toward an odour source and, for the dual choice tests, which of the two sources she would choose.

For the single odour source tests, 8 females were tested to each source on a given day (replicated 5 times). For dual choice tests, 10 females were individually tested to three odour source combinations on a given day (replicated 4 or 5 times). The position of the odor source chambers was switched each time after the first 5 wasps were tested.

In preliminary tests, a total of 20 experienced females were allowed to fly with only a piece of wet cotton used inside the odor source chamber. Some of the wasps would fly upwind, but none approached or landed on the odour release chamber.

Statistics. The results from single source bioassays were analyzed by analysis of variance after angular transformation, followed by Duncan's multiple range test. All results from the dual choice tests were compared using chi-square. In all cases $\alpha < 0.05$ was used to determine significant differences.

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Results

Single choice tests. No significant difference in attractiveness was found between water-washed host-damaged leaves and a complete plant-host complex when tested as single odour sources in the flight tunnel (Fig. 2). Frass and host larvae were attractive as well, but significantly less than the leaves and the plant-host complex.

Dual choice tests. The above results were confirmed in dual choice tests where in different combinations, two of the three components of a complete plant-host complex were tested parallel to each other in the flight tunnel (Fig. 3a). The damaged leaves were clearly more attractive than either frass of larvae, and frass was found to be more attractive than starved larvae. This ranking of attractiveness was also evident in the number of incomplete flights (females that did not reach the odour source). When the choice was between leaves and frass, the number of incomplete flights was the lowest, whereas it was the highest when frass and larvae were tested next to each other.
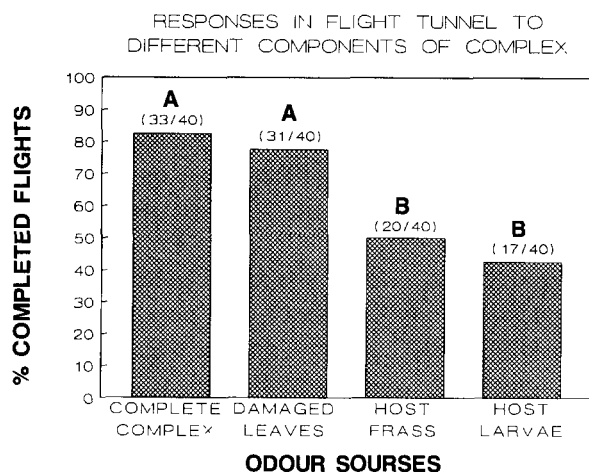

RESPONSES IN FLIGHT TUNNEL TO
DIFFERENT COMPONENTS OF COMPLEX

Fig. 2. Flight responses by *C. marginiventris* females to a complete plant-host complex, compared with flight responses to single components of a plant-host complex. The bars indicate percentages of completed flights toward a source (n = 40). With each bar, the actual fraction of females flying to the source is shown, while letters indicate significant differences in attractiveness between the odour sources (Duncan's multiple range test after analysis of variance, P < 0.05).

Recombinations of odour sources. The host-damaged leaves were recombined with either one of the two other components to determine whether any combination would be more attractive than the damaged leaves alone. It was found that adding back the frass made no difference, but that damaged leaves plus larvae (most of them feeding on the leaves) were significantly more attractive than damaged leaves alone (Fig. 3b). Consistent with that, damaged leaves plus larvae were more attractive than damaged leaves plus frass.

The effect of larval feeding. Starved larvae alone were the least attractive, but when recombined with damaged leaves they caused a significant increase in attractiveness, therefore, it was hypothesized that the additional feeding damage caused by the larvae was required to have this effect. To test the effect of larval feeding, the recombination of damaged leaves plus larvae was compared with a similar odour source in which the larvae were prevented from feeding by keeping them in a brass screen cage (0.5 mm mesh) inside the glass cylinder next to damaged leaves. Indeed, the source with the actively feeding larvae was more attractive than the source with the caged larvae (Fig. 3c), and, when a source of damaged leaves with caged larvae was compared with just damaged leaves, the odour sources were equally attractive. Attraction to a complete recombination of a plant-host complex (including frass and feeding larvae) was statistically equivalent to an odour source with only feeding larvae on damaged leaves (Fig. 3c).

Controls. The release of the active volatiles may have been affected by taking apart the complete plant-host complex. To determine whether the procedure that we used decreases the attractiveness, a recombined plant-host complex was tested alongside a complete plant-host complex that was not previously taken apart. The first part of Fig. 4 shows that the recombined complex was not less attractive than an untreated complete complex. In fact, the recombined complex was slightly more attractive, perhaps because it contained starved larvae that ate more vigorously.

DUAL CHOICE TESTS IN FLIGHT TUNNEL

a

INCOMPLETE
FLIGHTS

25		8		7
*	LEAVES	FRASS		

3		18		19
	LARVAE	FRASS	*	

24		3		13
*	LEAVES	LARVAE		

b

22		18		10
	LEAVES	LEAVES - FRASS		

11		30		9
	LEAVES	LEAVES + LARVAE		

12		30		8
	LEAVES - FRASS	LEAVES - LARVAE	*	

c

15		28		7
	CAGED LARV. + LEAVES	LARVAE + LEAVES	*	

21		18		11
	CAGED LARVAE + LEAVES	LEAVES		

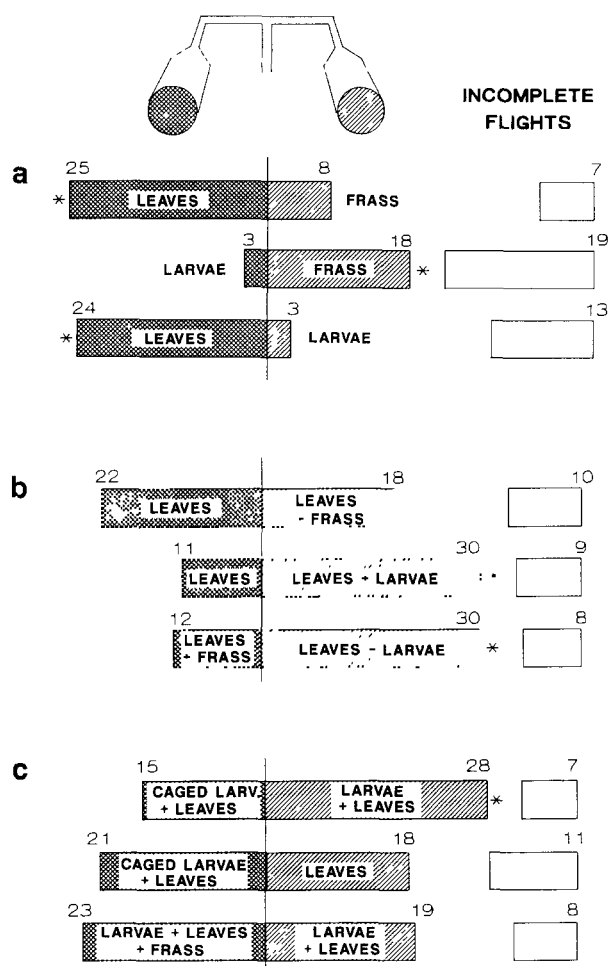| 23		19		8
	LARVAE + LEAVES + FRASS	LARVAE + LEAVES		

Fig. 3. Flight responses by *C. marginiventris* females during dual odour source tests. Two hatched bars show the fractions of females that chose a particular odour in each combination. The open bar to the right of each combination represents the females that did not fly to either of the two odour sources. Given with each bar is the actual number of females that they represent. The asterisks indicate significant preferences for particular odours ($\chi^2 df_1$, $P < 0.005$).
LEAVES = 3 water-washed corn seedlings that were fed upon by BAW larvae overnight.
FRASS = BAW by-products wiped off of the host-damaged corn seedlings.
LARVAE = 15 starved and water-washed early third instar BAW larvae.
a. Responses to single components of a complete plant-host complex, tested in combinations of two.
b. Responses to host-damaged leaves compared with different recombinations of damaged leaves with either frass or larvae.
c. Testing for the importance of larval feeding in attracting *C. marginiventris* females.

DUAL CHOICE TESTS IN FLIGHT TUNNEL

INCOMPLETE
FLIGHTS

19		23		8
	COMPLETE COMPLEX	LARVAE + LEAVES+FRASS		

5		34		11
	UNDAMAGED LEAVES	DAMAGED LEAVES	*	

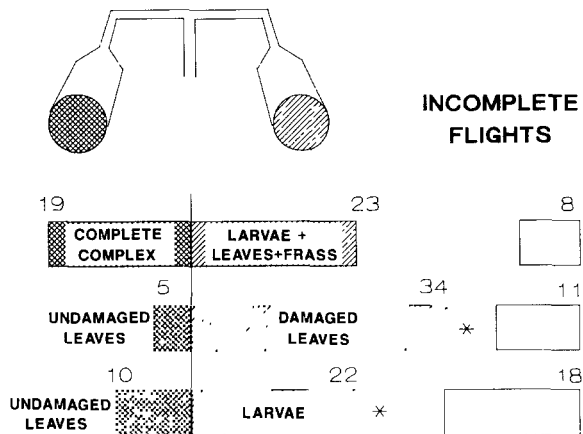| 10		22		18
	UNDAMAGED LEAVES	LARVAE	*	

Fig. 4. Control dual choice tests. The first combination shows the effects of the experimental procedure on the attractiveness of the odour sources. The other two combinations show the relative attractiveness of undamaged corn seedlings. For further details, see the text and the legend with Figure 3.

Finally, undamaged corn seedlings were tested for their attractiveness. Compared to damaged leaves, they were far less attractive. Even when undamaged leaves were tested alongside an odour source that consisted only of larvae, undamaged leaves were far less attractive (Fig. 4).

Discussion

Host-damaged corn seedlings were found to be the primary source of volatile semiochemicals that attract females of *C. marginiventris*. Yet, a significant number of females were observed to fly to an odour source containing frass only as well as to a source with larvae only (Fig. 2). However, when they were tested in choice situation, the relative importance of these two components of a complete plant-host complex in attracting *C. marginiventris* appeared to be minor (Fig. 3a). Moreover, the amounts of frass used in the bioassays were unrealistically high since in the field most of the frass will drop to the ground.

Undamaged plants were far less attractive than plants damaged overnight by BAW larvae (Fig. 4). Strongest attraction was observed when larvae were put back on the already damaged corn seedlings (Fig. 3c). This was not clear from the

single choice tests which showed no statistical difference between a complete plant-host complex and damaged leaves alone. In dual choice tests, however, a clear difference was found. It appears that choice tests are more suitable to reveal relative importance of different odour sources in attracting an organism. However, dual choice tests alone may not reveal those cases where different steps of an organism's searching behaviour are evoked by specific chemicals from different sources. In other words, if two sources are tested together, one of them may induce initial upwind flight while the other source results in close range attraction. This might not always be recognized unless both single source and choice tests are performed.

C. marginiventris attacks many different host species (at least 20) on a wide range of plants. It could therefore be presumed that this wasp innately responds to compounds that are common to most green plants, such as 'greenleafy odours' (Visser *et al.*, 1979). During foraging experiences the female wasps appear to learn to respond to odour blends that are specific for a certain plant-host complex (Turlings *et al.*, 1989, 1990). Turlings *et al.* (1990) not only showed that *C. marginiventris* can distinguish between the odours of two different plant species fed upon by the same host species, but also between two different host species feeding on the same plant species. Based on those findings and the data from this study, we suggest that, due to different feeding characteristics, different host species may cause a differential release of plant compounds which can be detected by the parasitoids after experience.

Plants are commonly found to be the sources of long-range attractants for parasitoids (Vinson, 1975; Nordlund *et al.*, 1988; Williams *et al.*, 1988). A well documented example is that of the ichneumonid parasitoid *Campoletis sonorensis* (Cameron) (Elzen *et al.*, 1983, 1984, 1986, 1987). Like *C. marginiventris*, *C. sonorensis* attacks many lepidopteran species. It is attracted to plants that are untouched by hosts, but damaged plants are far more attractive than undamaged plants (Elzen *et al.*, 1983). In preliminary experiments, *C. mar-*

giniventris females were also observed to fly to and land on undamaged plants, but the slightest, even artificial damage, would increase responsiveness and wasps would fly directly to the damaged sites. For the generalist parasitoids *C. marginiventris* and *C. sonorensis*, plants are clearly the main source of volatile attractants that not only guide these wasps into areas that may harbor hosts, but also serve to get them into the direct vicinity of the host. Once a wasp reaches a micro-habitat of its host, it may rely on contact kairomones present in the by-products of the host, such as silk and frass, for the final step of host location.

The more specialized parasitoid *Microplitis croceipes*, which attacks only *Heliothis* spp. is also attracted to the food plants of its hosts (Elzen *et al.*, 1987; Eller *et al.*, 1988; Drost *et al.*, 1988), but host feces are the key source of odours that attract this wasp to the micro-habitat of its hosts (Eller *et al.*, 1988; Elzen *et al.*, 1987). In general, plant odours appear to play a major role in the host searching process of parasitic insects (Nordlund *et al.*, 1988).

Parasitization by *C. marginiventris* dramatically reduces the amount of damage a larva will do to plants (Ashley, 1983; Jalali, 1988). Such advantages that plants may enjoy from attracting parasitoids when under attack by herbivores, make them likely sources of synomones. Natural selection is expected to favor plants that attract entomophagous insects (Dicke & Sabelis, 1988b; Sabelis & de Jong, 1988), while it would minimize the release of reliable chemical cues by the phytophagous prey or hosts. Several authors have recognized the possible sophisticated tritrophic relationship that may have resulted from these selective pressures (*e.g.* Vinson 1976, 1981; Vinson *et al.*, 1987; Price *et al.*, 1980; Price 1981). Recently, their ideas were confirmed in several elegant studies conducted by Dicke and coworkers. These studies revealed that spider mite infested plants play an active role in the attraction of predatory mites (Dicke & Sabelis, 1988b; Dicke *et al.*, 1990a, 1990b). Future combined chemical and behavioral studies will explore the complexity of a similar relationship between *C. marginiventris* and the plants its hosts feed on.

Acknowledgements

Résumé

Plantes endommagées par des chenilles: source de synomones volatiles guidant le parasitoïde Cotesia marginiventris *vers le micro-habitat de ses hôtes*

L'hyménoptère *C. marginiventris* Cresson, parasite solitaire, est connu comme étant attiré par les odeurs liées à l'hôte émises par un complexe de chenilles consommant des feuilles. La source exacte de ces substances attractives restait encore à déterminer. Pour cela, des expériences en tunnel de vol ont été réalisées dans lesquelles différents composés du complexe plante et hôte ont été testés individuellement et en combinaisons diverses. Les 3 composés testés ont été:
1) des plantules de maïs endommagées par des chenilles de *Spodoptera exigua* (BAW);
2) des excréments produits par les chenilles de BAW consommant du maïs;
3) des chenilles de BAW en l'absence de plantes et d'excréments.

Les plantes endommagées ont été significativement plus attractives que les excréments ou les chenilles. En expériences de choix, les excréments étaient plus attractifs que les chenilles. Différentes combinaisons de ces 3 composantes principales ont montré que l'attractivité augmentait quand les chenilles étaient associées à des feuilles endommagées. Ajouter des excréments n'augmentait pas significativement l'attractivité. Quand des chenilles étaient associées avec des feuilles endom-

magées, mais en présence d'écran les empêchant de consommer les feuilles, l'attractivité était celle des feuilles endommagées seules. Des feuilles de maïs n'ayant jamais été exposées aux dégâts des chenilles étaient à peine attractives. On peut en conclure que les feuilles endommagées par les chenilles sont la principale source de substances volatiles qui orientent le parasitoïde *C. marginiventris* vers le voisinage de ses hôtes. La consommation active par les chenilles augmente probablement la quantité de substances émises par les plantes, ce qui se traduit par une attractivité accrue. Les substances volatiles des plantes jouent un rôle dans la découverte de l'habitat de l'hôte par les parasitoïdes. De plus en plus d'éléments suggèrent qu'une interaction sophistiquée entre hôte, plante et parasitoïde sera éventuellement révélée.

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